feedback from the periphery influencing the export of transmitter from the cell body and that each branch contributes to this feedback in proportion to the amount of transmitter it ordinarily transports.

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11. The PLN synapses are about 24 mm from the cell body of GCN, and serotonergic vesicles are transported at a rate of 48 mm per day at 14°C (*3*), so surplus vesicles would not reach the synapses until 12 hours after transection of the CBC. A signal moving back by retrograde transport would take another 12 to 24 hours to reach the cell body.
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Electric and Magnetic Field Detection in Elasmobranch Fishes

Abstract. *Sharks, skates, and rays receive electrical information about the positions of their prey, the drift of ocean currents, and their magnetic compass headings. At sea, dogfish and blue sharks were observed to execute apparent feeding responses to dipole electric fields designed to mimic prey. In training experiments, stingrays showed the ability to orient relative to uniform electric fields similar to those produced by ocean currents. Voltage gradients of only 5 nanovolts per centimeter would elicit either behavior.*

The shark *Scyliorhinus canicula* and the skate *Raja clavata* have shown a remarkable sensitivity to electric fields in the seawater environment (*1*). The skate exhibited cardiac responses to uniform square-wave fields of 5 Hz even at voltage gradients of 0.01 μV/cm (*2*). The sense organs that detect the electrical stimuli were identified as the ampullae of Lorenzini by the method of selective denervation (*3*) and by recording from the afferent nerve fibers (*4*). Physical theory and behavioral evidence suggest that the elasmobranchs use the electric sense both in predation and for the detection of orientational cues (*5, 6*).

The role of the electric sense in predation was inferred from measurements on the bioelectric fields of fishes and from experiments in which (i) prey fish were shielded with agar to attenuate all but the electrical cues and (ii) the bioelectric fields of prey were simulated by passing electric current between two closely spaced electrodes (*2, 5*). Both *S. canicula* and *R. clavata* executed well-aimed feeding responses to the agar-screened prey and to dipole fields of frequencies from 0 to about 8 Hz (*6*).

In early investigations, the sharks and skates were tested in polyvinyl pools to avoid interference from ambient electric fields. The validity of those results was confirmed by studies at sea, made from a research vessel free of galvanic fields and fitted with a viewing well. Attacks on real and electrically simulated prey were observed in the smooth dogfish *Mustelus canis* and the blue shark *Prionace glauca* in the waters off Cape Cod, Massachusetts (*7*).

Mustelus canis was attracted by liquefied herring released from a tube in the center of the research area. Prey fields were simulated by applying direct current to a pair of electrodes to the right or left of the odor source (Fig. 1A). The tube and electrodes were fitted from beneath through holes in a polyvinyl plate that was set into the bottom and camouflaged by glued-on sand. For young dogfish (30 to 40 cm), an 8-μA current was passed between electrodes 2 cm apart (d_1 electrodes, Fig. 1A) and 15 cm from the odor source. For larger dogfish (90 to 120 cm), the current was switched to electrodes 5 cm apart (d_2 electrodes, Fig. 1A) and 30 cm from the odor source. Tests were conducted at night, when the animals were foraging for food. The setup, located at depths of 2.5 to 3.5 m, was dimly lit by underwater lights.

The attacks usually started with a sudden dive or turn, making them suitable for assessing the distances of response and the corresponding stimulus strengths. With the electric current spreading into half-space, the field along the dipole axis measured $\rho Id/\pi r^3$ μV/cm (for $r >> d$), where ρ is the resistivity of seawater (23 to 26 ohm-cm), I the applied direct current (8 μA), d the electrode spacing (2 or 5 cm), and r the recorded length of the radius vector with the dipole as origin. In the plane normal to the dipole, the field strength was only half that of equidistant points along the dipole axis. The use of a constant-current source and salt bridges (50 cm long) eliminated the adverse effects of polarization at the stainless-steel electrodes. To prevent loss of continuity from air bubbles accumulating, the salt bridges were filled with seawater agar or threaded with seawater-soaked cotton wicks.

The dogfish approached singly or a few at a time and, although motivated by scent, they almost invariably attacked the electrodes between which current was passed and seldom bit the control electrodes or the odor source. In 49 out of 136 responses, small dogfish initiated their well-aimed dives from distances of 15 cm and more, sensing voltage gradients $\leq$0.033 μV/cm; in 16 of the responses, they struck from 18 cm or more, detecting gradients $\leq$0.021 μV/cm (Table 1). Larger dogfish initiated 44 out of 112 attacks from 30 cm and farther, where fields measured $\leq$0.010 μV/cm; in 15 of the responses the distances were in excess of 38 cm, revealing a sensitivity to ~ 0.005 μV/cm or 5 nV/cm (Table 2). Because the field strengths reported were those measured along the dipole axis, 5 nV/cm is a conservative estimate.

The relatively short response distances may suit the shark's feeding strategy (*8*). *Mustelus canis* frequently snapped at small fishes hovering over the sand, but most prey were alarmed in time to escape. The dogfish are not particularly fast-moving and, to catch their prey, they have to strike from close by and with great accuracy. For the detection of prey hiding in loose gravel or sand, it is not so much the distance of response as the penetration power that gives the electric sense an edge over other sensory modalities. It is noteworthy that, when both dipole pairs were activated, small dogfish avidly attacked the closely spaced electrodes, but often

Table 1. Attacks of small dogfish (*Mustelus canis*) on electrically simulated prey. Fields were produced by a current of 8 μA passed between two electrodes 2 cm apart (at a seawater resistivity of ~ 23 ohm-cm). The distance of response was defined as the length of the radius vector from the center of the dipole to the position at which the shark initiated the attack. Abbreviations: P, responses for which the radius vector was approximately parallel to the dipole axis; N, responses for which the radius vector was approximately normal to the dipole axis; and I, responses from intermediate directions. The voltage gradients given are those for the P direction. In the I and N directions the gradients were weaker by a factor 1 to 1/2.

Distances of response (cm)*	Number of responses			Voltage gradients (nV/cm)
	P	I	N	
< 15.2		87†		> 33.1
15.2 to 17.8	8	22	3	≤ 33.1
17.8 to 20.3	2	3		≤ 20.8
20.3 to 22.9	1	3		≤ 14.0
22.9 to 25.4		2		≤ 9.8
25.4 to 27.9		2		≤ 7.1
27.9 to 30.5	1			≤ 5.4
30.5 to 35.6				≤ 4.1
≥ 35.6	1	1		≤ 2.6

*Metric equivalent of integral number of inches.
†Total of P, I, and N responses.

avoided the widely spaced electrodes that simulated larger prey.

Research on *P. glauca* was carried out in water 40 m deep, 25 km south of Martha's Vineyard, Massachusetts. The odor source and electrodes were attached to a horizontal spreader bar that was suspended at a depth of 5 m under the viewing well (Fig. 1B). Two dipoles (d_1 and d_2, Fig. 1B), each with the electrodes 5 cm apart, were mounted 30 cm from the odor source and embedded in open-mesh sponges to present the sharks with distinct targets. A direct current of 8 μA was applied to one dipole at a time, producing a full-space field half as strong as the half-space field used for the larger dogfish. To prevent the setup from disturbing the sharks, the underwater gear was made simple and inconspicuous, lowered deep beneath the boat, and only dimly lit.

During one calm night of data collecting, four to five blue sharks, 2 to 3 m in length, repeatedly circled the apparatus and attacked a total of 40 times. Two of the bites occurred at the odor source, seven at the control electrodes, and 31 at the prey-simulating electrodes. Because the blue sharks moved in gradually, the distances from which they attacked were difficult to gauge. Three nights of working in rougher seas yielded ten more attacks, of which the electrically active target received nine and the control electrodes only one. The blue sharks, like the bottom-dwelling dogfish, obviously preferred the prey-simulating field to either the control electrodes or the odor source.

Research on the orientation to electric fields of inanimate origin has evolved along two lines of thought (*6*), both inspired by Faraday's 1832 lectures on electricity (*9*). The electric fields induced by ocean currents flowing through the earth's magnetic field might help elasmobranch fishes compensate for drift, follow the currents, or orient in familiar territory (passive electro-orientation). The electric fields that the animals induce by swimming through the earth's magnetic field may allow them to detect their magnetic compass headings (active electro-orientation). In both instances, the voltage gradients range from ~ 0.05 to 0.5 μV/cm (*6, 10*). Locally, fields of geochemical origin may add to those induced by motion through the earth's magnetic field (*6*).

Captive sharks and rays often orient spontaneously to directional cues, but reinforcement of the response usually leads to more reproducible data. To test the ability of elasmobranch fishes to use the direction and polarity of uniform electric fields, the stingray *Urolophus halleri* was conditioned to seek reward (a small piece of herring) by selecting one of two corrals on opposite sides of a shallow, circular tank, where the correct corral was arbitrarily chosen as the one on the left relative to the field (Fig. 1, C and D) (*11*). Because the stingrays also detect the ambient magnetic field (*12, 13*), tests were conducted (i) in a null magnetic field, (ii) in the presence of only the vertical component of the earth's magnetic field, and (iii) in the undisturbed earth's magnetic field.

Table 2. Attacks of large dogfish (*Mustelus canis*) to electrically simulated prey. Fields were produced by passing 8 μA between electrodes 5 cm apart. For further explanation, see legend to Table 1.

Distances of response (cm)	Number of responses			Voltage gradients (nV/cm)
	P	I	N	
< 30.5		68*		>10.3
30.5 to 33.0	7	15		≤ 10.3
33.0 to 35.6	2	1		≤ 8.1
35.6 to 38.1		4		≤ 6.5
38.1 to 40.6		1	1	≤ 5.3
40.6 to 43.2		4		≤ 4.4
43.2 to 45.7		2		≤ 3.6
45.7 to 48.3	3	1		≤ 3.1
48.3 to 50.8				≤ 2.6
50.8 to 53.3		1	1	≤ 2.2
≥ 53.3			1	≤ 1.9

*Total of P, I, and N responses.

Electric fields were produced by passing direct current of uniform density through the body of seawater (Fig. 1C). The current entered and left the system by two stainless steel electrodes housed in plastic bottles. Two sets of 18 salt bridges connected the bottles to the main volume of water. To spread the current uniformly, the salt bridges were evenly spaced along the circumference of the tank and cut to lengths inversely propor-

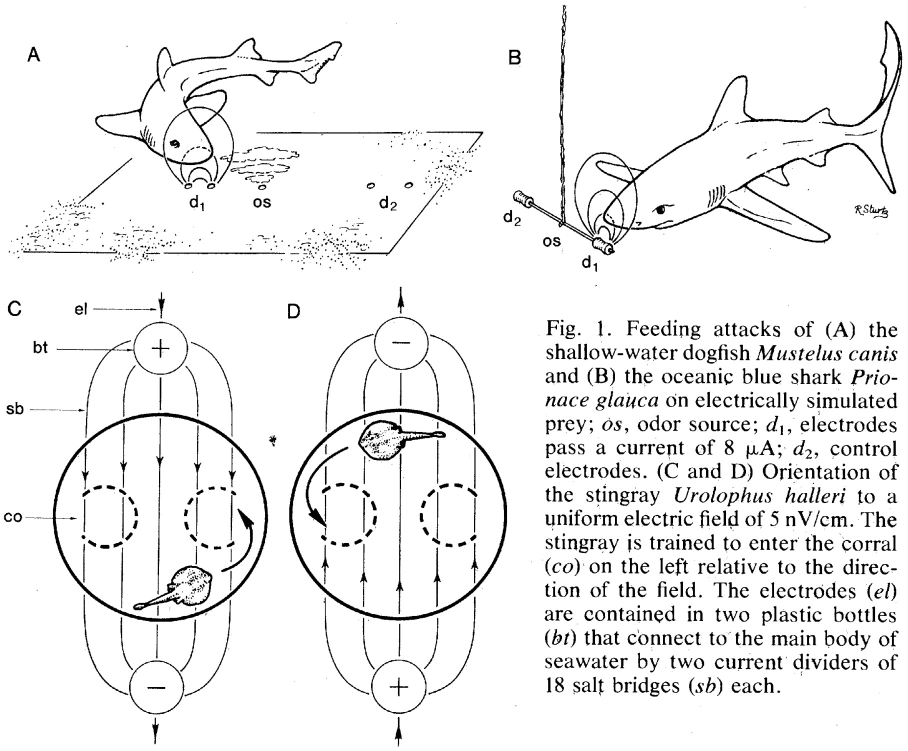

Fig. 1. Feeding attacks of (A) the shallow-water dogfish *Mustelus canis* and (B) the oceanic blue shark *Prionace glauca* on electrically simulated prey; *os*, odor source; d_1, electrodes pass a current of 8 μA; d_2, control electrodes. (C and D) Orientation of the stingray *Urolophus halleri* to a uniform electric field of 5 nV/cm. The stingray is trained to enter the corral (*co*) on the left relative to the direction of the field. The electrodes (*el*) are contained in two plastic bottles (*bt*) that connect to the main body of seawater by two current dividers of 18 salt bridges (*sb*) each.

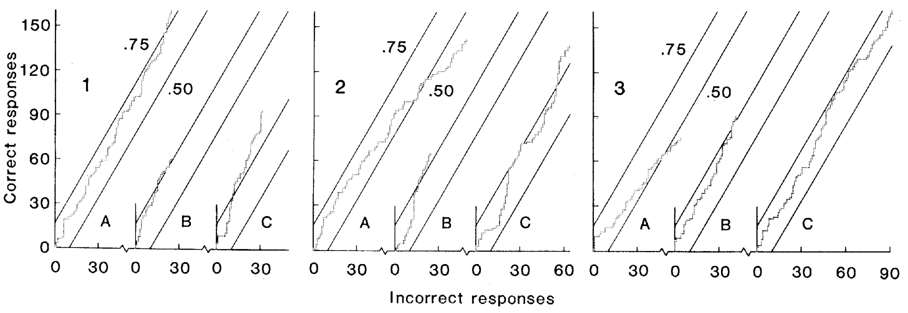

Fig. 2. Results of stingray orientation experiments as evaluated by sequential analysis. Stingrays 1, 2, and 3 were conditioned to orient with respect to uniform electric fields of 5 nV/cm under various magnetic conditions: (A) in a magnetic null field, (B) in the presence of only the vertical component of the earth's magnetic field, and (C) in the normal earth's magnetic field as measured in the southern California area where the rays were collected. The α and β errors associated with acceptance of orientation (.75 or three out of four, upper critical line) and rejection of orientation (.50 or random, lower critical line) were both set at .001.

tional to cosine α, where α is the angle between the electric field vector and the normal to the wall surface. A circular, wide-meshed plastic fence kept the animals from coming too close to the salt-bridge tubes. At a tank diameter of 1.8 m, a water depth of 15 cm, and a resistivity of 22.5 ohm-cm, a total of 0.6 μA sufficed for the threshold field (5 nV/cm). Inside the fence, the field was uniform to within 5 percent (*14*). The magnetic field was controlled by two single-axis Helmholtz coils.

Stingrays were tested two or three at a time, which allowed them to interact competitively. They earned a food reward for entering the correct enclosure, and a gentle prodding for an incorrect choice. Before each trial, the polarity of the field was selected randomly to prevent the use of nonelectrical cues. The experiments began at field strengths common in ocean waters, either 0.16 or 0.08 μV/cm (*10*). After each series, the voltage gradient was lowered by a factor of two until the stingrays failed to orient.

Orientational performances were evaluated by the sequential probability ratio test (*13, 15*). The null hypothesis H_0 was defined by a random or 50 percent correct choice, and the alternative hypothesis H_1 by a three out of four or 75 percent correct choice. The risks of erroneously rejecting or accepting H_0 were both set at $\alpha = \beta = .001$. In conformity with the usual procedure in sequential analysis, it was decided after each trial whether to accept the null hypothesis, to reject it, or to collect more data. The results of the series at 5 nV/cm (Fig. 2) showed that the first stingray oriented electrically, at $P \leq .001$, under all three magnetic conditions (218, 59, and 47 trials, respectively); that the second stingray failed to orient in the null magnetic field (171 trials), but did orient electrically in the presence of the vertical and the normal magnetic fields (62 and 77 trials, respectively); and that the third stingray was random in the null field (113 trials), oriented electrically in the vertical magnetic field (121 trials), and did not reach either critical level in the normal magnetic field (289 trials). At a field strength of 2.5 nV/cm, orientation was random in all three fish.

It should be emphasized that a successful performance would be extremely unlikely, at set criteria, if the fish were actually unable to orient to the field, whereas a lack of orientation need not contradict the animal's capabilities. However, whether elasmobranchs actually apply their electric sense to the detection of ocean currents and territorial cues must still be verified at sea. That the stingrays are able to distinguish the imposed electric fields from the usually much stronger fields that they induce by moving through the earth's magnetic field also suggests a familiarity with the latter and is consistent with the hypothesized electromagnetic compass sense (*12, 13*).

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Correlations Perceived and Measured

Cleveland, Diaconis, and McGill (*1*) describe three related experiments in which groups of subjects of some to presumably great sophistication about statistical procedures were asked to judge, by the "eyeball method," linear association of synthetic two-dimensional scatterplots. The diagrams were constructed to reflect significant scale (point-cloud size) variation at constant degree of association, for a range of degrees of association (*2*).

The results of all three experiments agreed that an increase in scale, which is manifest in decreased point-cloud size, is usually accompanied by increased judged association; furthermore, the two quantitative studies indicated that perceived degree of association does not appear to be a simple function of the most familiar statistic, the correlation coefficient. Cleveland *et al.* suggest several explanations for the scale effect, including perceived properties of the scatterplot ellipses and point size relative to display area dimensions, but they appear to overlook a simpler explanation which ultimately bears on the second result, that is, the role of the correlation coefficient, as well.

This concerns the perceptual influences of the axes and whether and how they are specified and located implies varying weights for the origin. Can the observer fail to note that the point cloud falls about the line $y = x$ and unconsciously add the origin as a fixed point [with greater effect the further the point